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ORIGINAL PAPER

Alien aquatic macroinvertebrates along the lateral dimension of a large floodplain

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Abstract Floodplains are simultaneously among the most species-rich and the most threatened ecosystems. Alien aquatic macroinvertebrates contribute to this threat but remain scarcely studied in the lateral dimension of floodplains. We modelled the realized ecological niches of the alien species occurring in 24 floodplain channels of the Rhône River. Environmental variables depicting the ecological niches were associated to the lateral hydrological connectivity and light availability, both being modified during floodplain restoration works. Eight alien species were observed and they demonstrated either ubiquity or a restricted niche, with no link to the date of introduction. For most of them, the main river channel appeared as an important dispersal route in the lateral dimension of the floodplain. An increase of both lateral connectivity and light availability favoured most of the modelled species. Consequently, we recommend that sector-scale restoration programmes preserve varying levels of lateral connectivity for floodplain channels to prevent the expansion of alien aquatic macroinvertebrates.

Keywords Ecological niche · Distribution modelling · Lateral hydrological connectivity · Light availability · Restoration · French Upper-Rhône River

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Introduction

Natural floodplains are among the world's most biologically productive and species-rich environments, encompassing characteristics of both terrestrial and freshwater systems (Sparks 1995; Tockner and Stanford 2002; Ward et al. 1999). Indeed, such ecosystems contribute to the exchange of nutrients and organisms among a large mosaic of habitats (Sparks 1995). They also provide important ecological and economic services. For instance, they serve as refuges and migration corridors for the fauna and they contribute to disturbance regulation, water supply and waste treatment. However, they are also among the most endangered ecosystems. For several decades, they have been subjected to major threats such as habitat alteration, flow and flood control, pollution, water abstraction, alien species introductions and overharvest (Sparks 1995; Tockner and Stanford 2002). At the hands of the increasing degradation of floodplain ecosystems, the last few decades have seen the assessment and implementation of various restoration strategies (Buijse et al. 2002; Lake et al. 2007; Palmer et al. 2005).

Rivers and their floodplains, due to human activities and alterations, are also subject to biological invasions (Kinzelbach 1995; Tockner and Stanford

2002). Even though the transport and introduction of alien species can occur naturally, interconnection of river basins through man-made canals and trade shipping has facilitated the introduction of alien aquatic macroinvertebrates to large rivers (Bij de Vaate et al. 2002; Devin et al. 2005). The alien aquatic macroinvertebrate species mainly belong to the mollusc and crustacean groups (Bernauer and Jansen 2006; Devin et al. 2005; Humpesch and Fesl 2005). As a consequence of these introductions in aquatic systems, Pimentel (2005) has documented the harmful impacts on the economy, society and the environment. The harmful impacts include the transport of viruses and pathogens, the damages and associated costs linked to electric power plants and water supply systems (Pimentel 2005), the modification of nutrient fluxes (Hall et al. 2003) and the homogenization of faunal assemblages (Bollache et al. 2004). Thus, important impacts can originate from the introduction of alien aquatic macroinvertebrate species and they can represent a threat to the integrity of aquatic ecosystems.

The French Upper-Rhône River and its floodplain exhibit a lower percentage of alien aquatic macroinvertebrate species compared with the downstream part of the river (Fruget 2003) and other large European rivers such as the Rhine and Danube (Bernauer and Jansen 2006; Humpesch and Fesl 2005). Nevertheless, this sector is located between two potential sources of colonisation: Lake Geneva upstream and the downstream part of the Rhône River, which is connected to the Rhine via the Saône River. Furthermore, after almost two centuries of embankment and hydro-power construction, the Upper-Rhône floodplain is currently being subjected to a hydrological and ecological restoration programme, which started in 2004 (see Mérigoux et al.(2009) for details of this restoration programme). As part of this programme, several floodplain channels were deepened or reconnected to the main channel, and forest harvesting and replanting have occurred. These modifications represent short-term disturbances of floodplain habitats (Lake 2000; Tockner and Stanford 2002) that can facilitate the spread of alien species through the enhancement of the connections between channels and the creation of new habitats open to colonisation.

In this context, this study aimed at assessing the distribution of alien aquatic macroinvertebrate species in the lateral dimension of a large floodplain, a topic seldomly addressed.

Besides the fact that the distribution of an alien species in a recipient ecosystem depends on characteristics of introduction, species and habitat conditions (Lockwood et al. 2007), we first expected that alien species established in the system for a longer time would have more defined habitat associations than later invaders. Indeed, the introduction phenomenon can be regarded as random. Propagules are released and must survive in the recipient environments that are not necessarily their optimal habitat (Lockwood et al. 2007). We can assume that an alien species introduced recently is potentially dispersed in several types of habitats (i.e. wide niche breadth) and progressively reaches its optimal habitat (i.e. narrower niche breadth) during a period of several years or decades after introduction.

Secondly, our goal was to demonstrate that the main river channel is an important pathway of dispersion for alien species. Finally, given the widespread attempts (in Europe and North America) to restore floodplain-river connections (Buijse et al. 2002; Paillex et al. 2009; Palmer et al. 2005), we aimed at predicting the impact of restoration works upon the distribution of alien species.

Methods

The study was conducted in 24 floodplain channels along a 45 km-long sector of the French Upper-Rhône River between the cities of Geneva and Lyon (Figs. 1, 2). Since 1980, two hydropower diversion dams (Belley and Brégnier-Cordon) comprising a head race, the power plant, a tail race and a by-passed section, were constructed in the braided plains of the studied sector (Roux et al. 1989). Nowadays, the annual average discharge in the sector is about 430 m^3/s. In this area, due to repeated glaciation phases, a large diversity of geomorphological patterns has been created. Consequently, the floodplain comprises a range of channels with varying levels of lateral connectivity with the main river: from the main channel to secondary channels permanently connected (eupotamal), channels connected at their downstream end (parapotamal), disconnected channels (plesiopotamal), abandoned meanders (paleopotamal) and wetlands (Roux et al. 1989). This variety of lotic and lentic habitats is exceptional

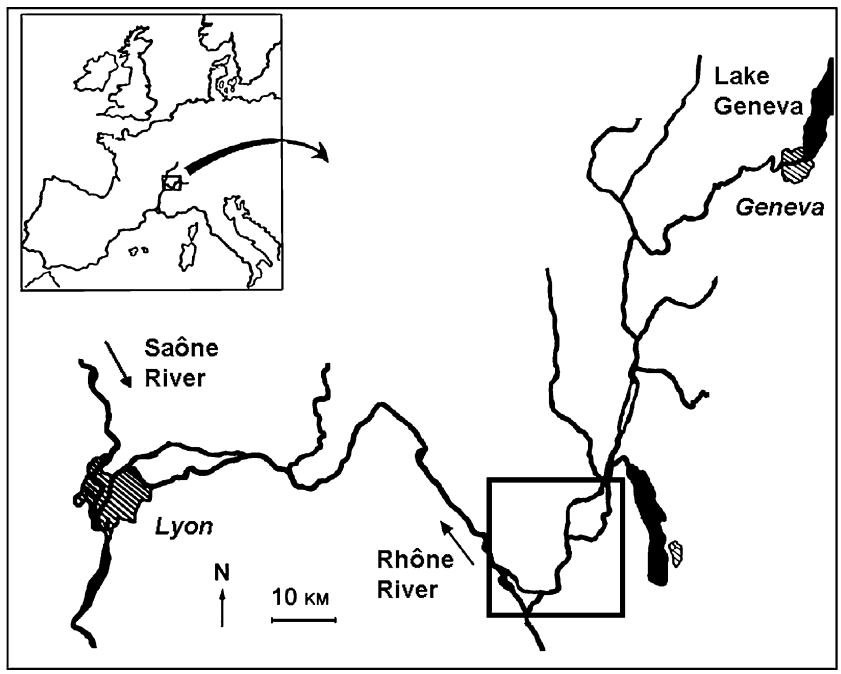

Fig. 1 Location of the French Upper-Rhône River and the two potential sources of colonisation: Lake Geneva and the Saône River. The study sector is framed

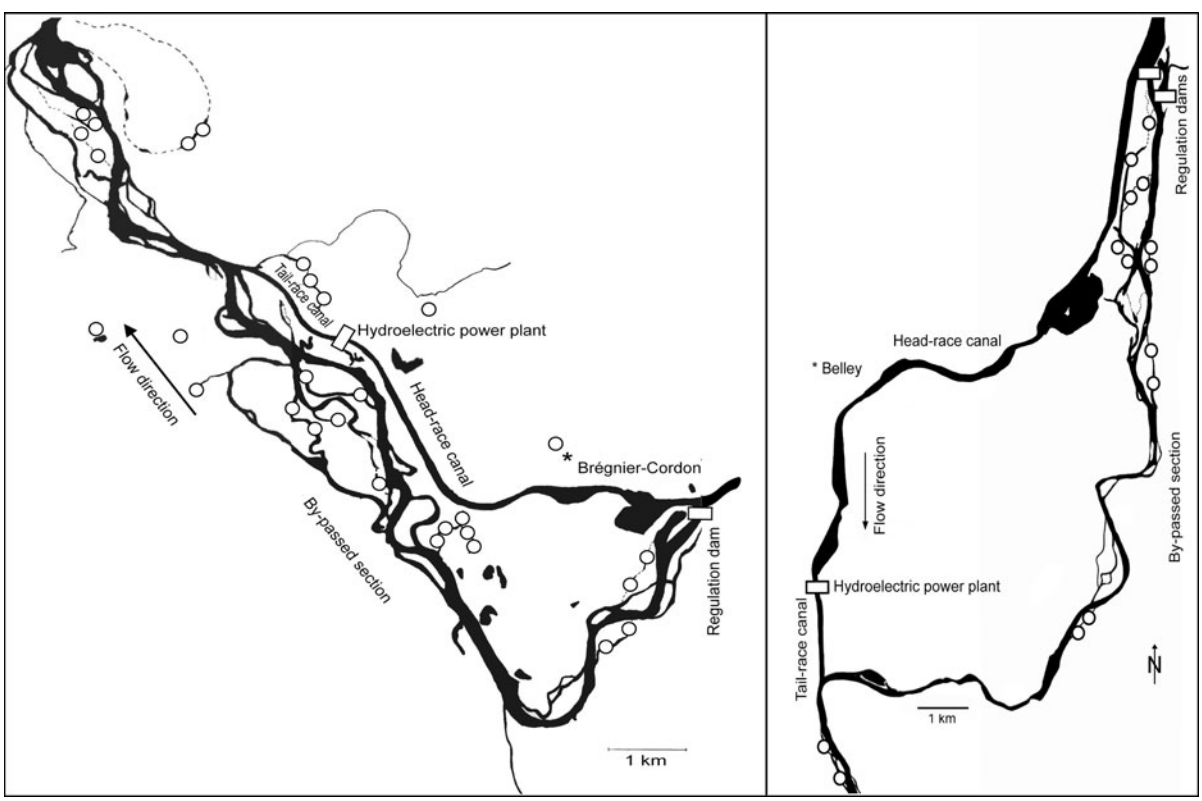

Fig. 2 Location of the floodplain channel sites (*circles*) sampled in the study sector

for the Rhône River which is much more degraded downstream.

Habitat variables, together with the macroinvertebrate samples, were collected according to a standardized method between 2002 and 2005, prior to restoration operations. Two sites were sampled per floodplain channel: one upstream and one downstream to take into account the diversity of habitat occurring in the channels. In two longer floodplain channels an additional third central site was designated. For each site, four sampling quadrats (0.5 × 0.5 m delimited by a metal frame) were set out randomly along a 30 m stretch.

Macroinvertebrates were sampled in spring (April–May) and summer (July–August) to account for seasonality. Within each quadrat, macroinvertebrates were collected with a hand net (opening: 9.5 × 14.5 cm; mesh size: 500 μm) by disturbing the substrate and the vegetation (in order to reach sufficiency, this process was performed three times). All the samples were then preserved in 70% ethanol. In the laboratory, macroinvertebrates were exhaustively sorted from each sample under a zoom microscope and identified to the species level where possible. A total of 328 samples (belonging to 50 sites) were sorted and determined. The number of individuals per m^2 for each species was expressed as an average per site and log-transformed to stabilize the variances.

We considered as "alien" species that did not originate from the Upper-Rhône floodplain and were introduced during the past 200 years (Devin et al. 2005). Among the diverse terminology used to qualify non-indigenous species (Colautti and MacIsaac 2004), we decided to use the term of "alien", according to the definition described in the European strategy on invasive alien species published by the Council of Europe in 2004 (Genovesi and Shine 2004). Moreover, we do not study explicitly the impacts of the introduction of alien species on biological diversity.

Six habitat variables were measured to express two functional aspects of the channels: (1) the lateral connectivity with the main river channel and (2) the light availability. (1) The organic matter content of the upper sediment, (2) the submerged vegetation cover, and (3) the mineral substrate diversity were chosen because they can be used as surrogates for the lateral hydrological connectivity (Paillex et al. 2007). (4) The solar access, (5) the perpendicular shading on the water surface by woody vegetation, and (6) the percentage of forest cover in the surrounding environment were selected because they express the light availability which is related to the heat balance of the channels (Davies-Colley and Payne 1998). The submerged vegetation cover and the mineral substrate diversity were measured in spring and summer at the quadrat level and expressed as averages at the site level, while the four other variables were measured directly at the site level. The shade, the forest cover and the solar access were only measured in summer. The benthic organic matter of the sediment (BOM) was measured from a core (28 cm^2 × 5 cm depth) taken in winter. All the material of the core was combusted for 90 min (loss on ignition at 560°C) (Rostan et al. 1987). The solar access (expressed in hours per year) was measured at the centre of each site using fish-eye lens photographs (Davies-Colley and Payne 1998; Denicola et al. 1992). The shade, the forest cover, the horizontal cover by submerged vegetation and the mineral substrate types (silt and clay, sand, gravel, pebble and larger) were assessed according to six cover categories: 0 (absence), 1]0–5%], 2]5–25%], 3]25–50%], 4]50–75%] and 5]75–100%]. The percentage of forest cover was assessed in 50 m-wide bands along both banks of each site. The percentual representation of the four mineral types was summarized as a Simpson diversity index. The organic matter percentage and the substrate diversity index were ($\log_{10}$ $(x + 1)$) transformed prior to analyses to stabilize variances.

Descriptive and predictive techniques (respectively OMI analysis and GAMs) were used to study the response of alien species to environmental variables. The former involved a two-table ordination technique, the Outlying Mean Index analysis (OMI) (Buisson et al. 2008; Dolédec et al. 2000; Mérigoux and Dolédec 2004), which investigates the separation of species niche along any spatial or temporal variation in given habitat conditions. It enables the assessment of species marginality, which corresponds to the niche deviation from the reference niche of a theoretical ubiquitous species in the same range of habitat conditions. Three niche parameters were computed: (1) the marginality index, (2) a tolerance or niche breadth index which is a measure of the niche breadth within the range of conditions considered and (3) a residual tolerance index, the part of the species distribution that cannot be explained by the habitat parameters involved (Dolédec et al. 2000). A

random permutation procedure tests if the overall niche segregation of all species is effective along the specific environmental gradient. The statistical significance of the marginality of each species is also tested with a random permutation test against the null hypothesis that the species is not significantly different from the theoretical ubiquitous species.

The second technique concerned the use of Generalized Additive Models (GAMs) (Hastie and Tibshirani 1990). These regression models express statistical relationships between a variable of interest (here species abundance) and environmental variables (explanatory variables). The diagnostic parameters for GAMs comprised: (1) a cross-validation based on the correlation ratio (r_2) between observed and predicted values, (2) the percentage of deviance of the response variable explained by the models. A Principal Component Analysis (PCA) was realized independently for each group of habitat variables in order to produce two explanatory variables corresponding to the lateral connectivity gradient (1st PCA) and to the light availability gradient (2nd PCA). In each PCA, the first factorial axis summarizing most of the information was kept as the explanatory variable. Consequently, the two variables entered in the models were composite "synthetic" variables. The GAMs estimate response curves with a non-parametric smoothing function, contrary to parametric terms, allowing for a closer matching to ecological data. For the response variable, the abundance of alien species, a quasi-Poisson family was used. A full-model selection was chosen in order to compare all predictor variables in the models of each species. Each response curve expressed the predicted species response to one of the variables in the absence of influence of the other variables. Calculations were performed with the GRASP (Lehmann et al. 2002) and the ade4 packages (Dray and Dufour 2007) for the R Software (Ihaka and Gentleman 1996).

Results

Alien species in the French Upper-Rhône floodplain

Eight alien species were identified within investigated sites. Most of them belong to the Crustacea and the Mollusca, with the exception of one Turbellarian (Table 1). *Physella acuta*, *Gyraulus parvus* and *Potamopyrgus antipodarum* were the most frequent and abundant in the samples (Table 1). The introduction periods of the eight species into the Upper-Rhône span approximately over 150 years. *Dreissena polymorpha* and *P. acuta* have been observed since the mid nineteenth century. *Orconectes limosus*, *P. antipodarum* and *Dugesia tigrina* first appeared in the sixties and seventies. *G. parvus* and *Corbicula fluminea* were collected for the first time in the nineties. *Crangonyx pseudogracilis*, observed for the first time in 2004 as part of this study, was the most recent alien macroinvertebrate species of the sector. The eight species cover a wide spectrum of hydraulic requirements, from rheophilous to limnophilous (Table 1). They also cover all the types of habitats from parapotamal to paleopotamal channels. According to results presented in Table 1, shipping is the most frequent vector of first introduction in Europe. More detailed information about introduction in the French Upper-Rhône River is missing (Table 1).

Niche analysis

The two groups of environmental variables were clearly distinguished in the OMI analysis (Table 2; Fig. 3). The first group (lateral connectivity) containing the substrate diversity (div), the organic matter (BOM) and the submerged vegetation cover (veg) was the most correlated to axis 1 (73% of the total explained marginality) and the most influential upon species niche differentiation. The second group (light availability) was the most correlated to axis 2 (25% of the total explained marginality), it contained the solar access (sol), the shade (sha) and the forest cover in the surrounding environment (for).

According to OMI results (Fig. 3), substrate diversity was the main factor explaining the abundance of *C. fluminea*, *O. limosus*, *D. polymorpha*, and *P. antipodarum*. *C. pseudogracilis* was mostly influenced by shade and for the three remaining species, the results were more complex, the species being influenced by combinations of BOM, submerged vegetation cover, and solar access.

Niche segregation in this set of species was significant along the two groups of variables. The overall random permutation test on the average marginality of the eight species was significant

Table 1 Eight alien species found in the 24 floodplain channels of the French Upper-Rhône

Groups	Families	Species	Geographic origin	First observation in the French Upper-Rhône	Vector of first introduction in Europe	Type of habitat where species were collected	Hydraulic Preferences	Frequency in the samples (%) ($n = 328$)	Mean number of individuals per sample (0.25 m^2)	Maximal number of individuals per sample (0.25 m^2)
Crustacea Amphipoda	Crangonyctidae	*Crangonyx pseudogracilis* (Bousfield, 1958)	North American	2004[a]	Shipping[i]	Plesiopotamal	Limnophilous[o]	0.6	0.01	1
Crustacea Decapoda	Cambaridae	*Orconectes limosus* (Rafinesque, 1817)	North American	1976[b]	Farming (intentional introduction)[j]	Parapotarnal	Rheo-limnophilous[p]	0.6	0.01	1
Mollusca Bivalvia	Dreissenidae	*Dreissena polymorpha* (Pallas, 1771)	Ponto Caspian	After 1852[c]	Shipping[k]	Parapotarnal	Indifferent[p] Rheophilous[q]	2.7	0.09	9
Mollusca Bivalvia	Corbiculidae	*Corbicula fluminea* (Muller, 1774)	Asian	1990[d]	Shipping[i]	Parapotamal to plesiopotama	Rheo-limnophilou[p] Indifferent[q]	5.5	0.22	18
Mollusca Gastropoda	Physidae	*Physella acuta* (Drapamaud, 1805)*	Mediterranean	1881[e]	(Inhabit Europe)[l]	Parapotamal to paleopotamal	Indifferent[p]	27.1	3.79	252
Mollusca Gastropoda	Planorbidae	*Gyraulus parvus* (Say,1817)	North American	1994[f]	Unknown	Parapotamal to paleopotamal	Limnophilous[p]	23.5	18.85	558
Mollusca Gastropoda	Hydrobiidae	*Potamopyrgus antipodarum* (Gray,1843)	New Zealander	1978[g]	Shipping[m]	Parapotamal to plesiopotamal	Indifferent[p] Limno-rheophilous[q]	14.9	249	154
Turbellaria	Dugesiidae	*Dugesia tigrina* (Girard 1850)	North American	1968[h]	Aquarists[n]	Parapotamal to paleopotamal	Limno-rheophilous[p] Rheophilous[q]	2.4	0.03	3

[a] This study (2002–2005)

[b] Stucki and Zaugg (2005)

[c] Germain (1930)

[d] Mouthon (2000)

[e] Locard (1881)

[f] Unpublished data of the authors

[g] Crozet et al. (1980)

[h] Russier and Lacombe (1970)

[i] Fruget (2003)

[j] Puky and Schad (2006)

[k] Khalanski (1997)

[l] Dillon et al. (2002)

[m] Morley (2008)

[n] Reynoldson and Young (2000)

[n] Piscart, Personal Communication

[o] Colling (1996)

[p] Mérigoux et al. (2009)

*The distinction between *P. acuta* and *P. heterostropha* is unclear and they might be the same species (Dillon et al. 2002). We kept the name *P. acuta* the oldest applied in the French Upper-Rhône

Table 2 Percentage of marginality explained and correlations between the environmental variables and the first two axes of the OMI analysis

OMI	Axis 1	Axis 2
% of marginality	73	25
bom[a]	−0.71	−0.01
veg[a]	−0.66	−0.08
div[a]	0.56	0.34
sol	−0.45	0.44
sha	0.24	−0.32
for	−0.07	−0.32

Sol solar access, *bom* organic matter, *veg* submerged vegetation cover, *for* forest cover, *sha* shade, *div* substrate diversity

[a] Indicates the most explained variables by the first axis of the OMI analysis

($P = 0.04$). Four of the eight alien species (*C. fluminea*, *G. parvus*, *P. acuta*, and *P. antipodarum*) demonstrated individually a significant niche marginality (Table 3), suggesting a significant influence of the selected environmental variables on their abundance (Table 3). *C. fluminea* and *P. antipodarum* showed a high deviation from the uniform distribution (48.2 and 65.8 OMI index respectively) indicating an important influence of the chosen variables. The tolerance (or niche breadth) values for *C. fluminea* and *P. antipodarum* were low (6 and 5.4 respectively). For *G. parvus* and *P. acuta*, the deviation from the theoretical uniformly distributed taxon was lower (32.9 and 6.8 OMI index respectively). The residual tolerance for these four species (28–49%) showed that other variables, not incorporated in this study, influenced their distributions.

Species showed a gradual replacement along the two variables the most correlated to each axis of the OMI analysis (BOM and solar access) (Fig. 4). An important disjunction was however observed between *G. parvus*, the species the most favoured by a high percentage of organic matter, and the four species observed in channels with less organic matter (Fig. 4a). With the exception of *O. limosus* and *C. pseudogracilis*, an important overlap was observed along the solar access variable (Fig. 4b). *C. pseudogracilis* appeared to be restricted to habitats with a limited solar access.

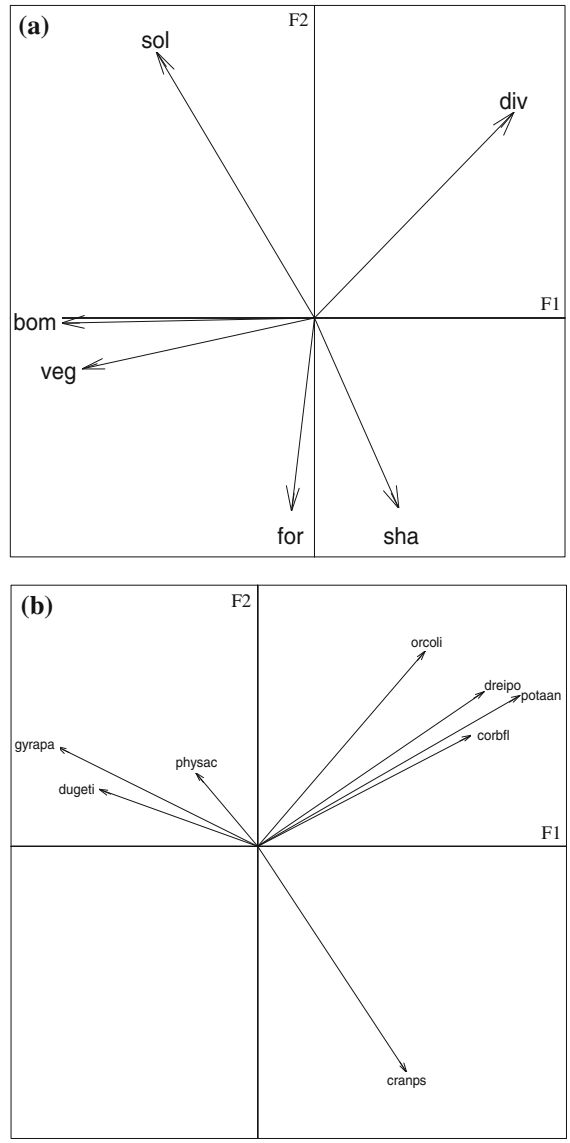

Fig. 3 OMI analysis of alien species niches: **a** PCA of environmental variables (sol (solar access), bom (benthic organic matter), veg (submerged vegetation cover), for (forest cover), sha (shade), div (substrate diversity)) and **b** weighted average positions of species (*arrow ends*) (see Table 3 for species codes). Each species position is proportional to the marginality index of that species. **a** and **b** results are along the two-first axes of the OMI analysis

Distribution modelling along environmental gradients

The part of the variance explained along the first PCA axis of the lateral connectivity variables was 70%

Table 3 Niche parameters of the eight alien species

Taxa	Code	OMI	Tol	RTol	*P* value
Corbicula fluminea	corbfl	48.2	6	45.8	0.03
Crangonyx pseudogracilis	cranps	93.8	0.5	5.7	0.24
Dreissena polymorpha	dreipo	66.4	1.4	32.2	0.11
Dugesia tigrina	dugeti	20.5	42.8	36.7	0.24
Gyraulus parvus	gyrapa	32.9	35.4	31.7	0
Orconectes limosus	orcoli	100	0	0	0.73
Physella acuta	physac	6.8	44.2	49	0.03
Potamopyrgus antipodarum	potaan	65.8	5.4	28.8	0

OMI Outlying mean index (%), *Tol* species tolerance (%), *Rtol* residual tolerance (%), *P* value statistical significance in the OMI analysis

(Table 4) and 69% along the first PCA axis of the light availability variables (Table 4).

GAMs were only calculated for the four most frequent species (*C. fluminea*, *P. antipodarum*, *P. acuta*, and *G. parvus*) with a frequency higher than 5%. Except for *P. acuta*, the cross-validation criteria for the model evaluation were higher than 0.5 (Table 5). The model for *C. fluminea* explained more than 60% of the total deviance of the species abundance. The first explanatory gradient (lateral connectivity variables) made the highest contributions in the models of *C. fluminea*, *P. antipodarum*, and *G. parvus*.

P. antipodarum and *C. fluminea* were positively influenced by an increase of the lateral connectivity whereas *G. parvus* was negatively affected by this gradient (Fig. 5). Regarding the light availability, *G. parvus* and especially *P. acuta* and *P. antipodarum* were favoured by an increase of this gradient. For *C. fluminea*, the effect of light availability was more complex with a U-shaped response curve.

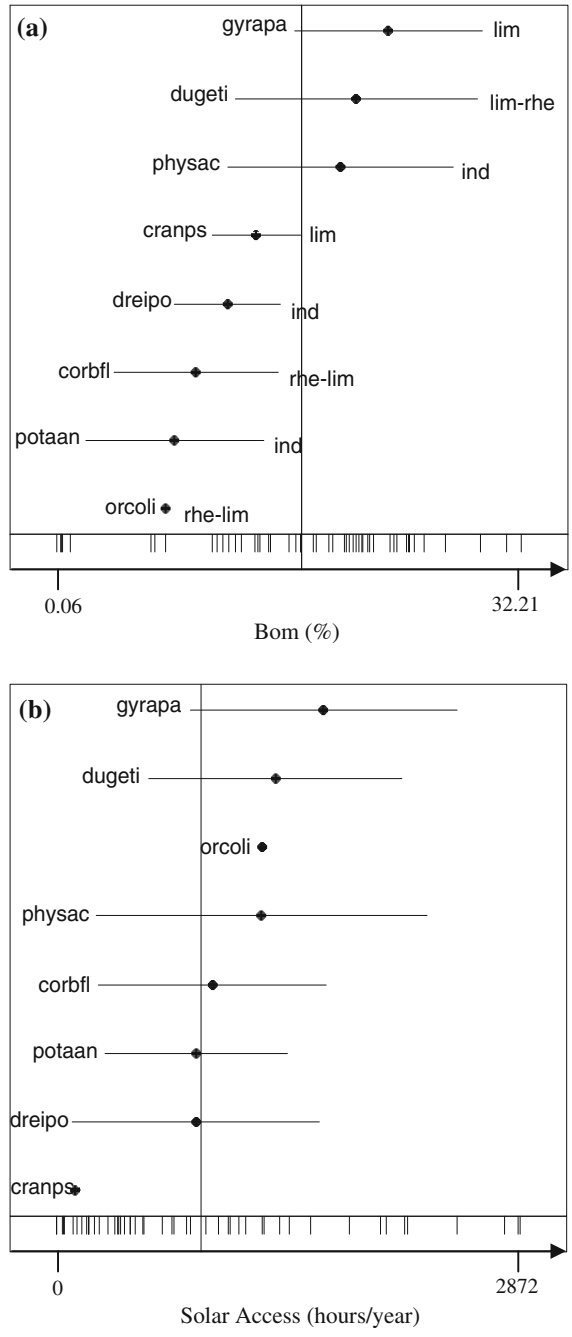

Fig. 4 Species positions along the main environmental variables bom (**a**) and solar access (**b**). Organic matter quantities in the sediment (Bom) are expressed in percentage. The solar access is expressed in number of hours of solar access per year. Lim, rhe and ind signify respectively limnophilous, rheophilous and indifferent, according to Colling (1996). The *horizontal line* for each species is the standard deviation. The *vertical line* is the mean for each variable

Discussion

Ecological niche of the alien species

For the four most abundant species, niche marginality was significant and GAM response curves differed between species. *C. fluminea* and *P. antipodarum* were influenced by substrate diversity. Indeed, Sousa et al. (2008) showed that *C. fluminea* prefers sandy

sediments mixed with silt and clay but could be found in all types of sediments. Similarly, Murria et al. (2008) noticed that *P. antipodarum* was observed in all substrate types (e.g. silt, sand, gravel, cobbles, and vegetation). These findings are in accordance with our results. As stated by Meier-Brook (2002), *G. parvus* inhabits pools, ponds or lakes. These observations also correspond to our results, which demonstrated that *G. parvus* was most abundant in channels with high organic matter content and vegetation cover, suggesting a low level of hydrological connectivity with the main river and limited or no disturbance by floods. With the exception of *P. acuta*, the three other modelled alien species found in the Upper-Rhône were therefore restricted to a defined range of conditions.

We expected that the species established in the system for a longer period would show a more restricted niche than later invaders. Indeed, *D. polymorpha*, which was the first alien species observed in the system, appeared specialized with the parameters we measured. Similar results were observed concerning the hydraulic preferences of this species in the main channel of the Rhône River. On the contrary, *P. acuta*, which arrived at the same period, presented a broader niche and appeared ubiquitous. *C. fluminea*, observed in the study sector recently (in the nineties), was significantly specialized. Therefore, there was no link between niche breadth and the date of first observation in the system. This outcome can be a

Table 4 Percentage of variability explained and correlations between the two groups of environmental variables and the first two axes of individual PCA

Gradients	Variables	Axis1	Axis2
Connectivity	% variability	70	20
	div	0.88	0.27
	bom	−0.87	−0.3
	veg	−0.76	0.65
Light	% variability	69	23
	sha	−0.9	−0.26
	for	−0.68	0.73
	sol	0.89	0.3

Connectivity corresponds to the lateral connectivity gradient whereas Light corresponds to the light availability gradient

Table 5 Dimensionless contributions of the two environmental variables (Connect: lateral connectivity, Light: light availability) in the GAM models, influence of increasing gradients on alien species and diagnostic parameters for GAMs

Taxa	Connect	Light	Cross-validation (r_2)	Explained deviance (%)
Corbfl	22.7 (+)	7.6 (±)	0.81	65.6
Potant	11.7 (+)	6.8 (+)	0.66	43.6
Gyrapa	4.6 (−)	3.5 (+)	0.59	34.8
Physac	1 (−)	2.5 (+)	0.44	19.4

(+) indicates a positive impact on species whereas (−) translates as a negative impact on species abundance

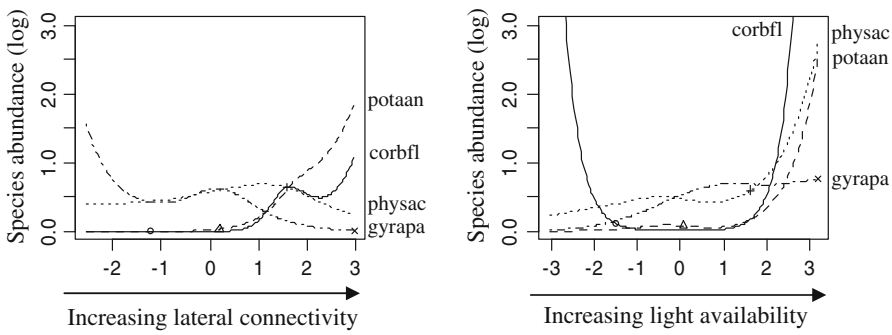

Fig. 5 Response functions for the log-transformed abundance of the four most frequent alien species along the two explanatory variables. The horizontal axis of each model expresses the coordinates of the sites along the first factorial axes of two separate PCA (lateral connectivity variables and light availability variables, respectively)

consequence of the evaluation of the first date of introduction, which can be either very precise or quite vague. Moreover, the species could have been introduced before the date of first observation. Another explanation for these findings can proceed from the intrinsic difficulties of modelling alien species distributions that can originate either in their rarity or in their potential ubiquity. Indeed, no GAM models were obtained for the four less abundant and less frequent species (*C. pseudogracilis*, *D. polymorpha*, *D. tigrina*, and *O. limosus*). According to OMI results, *P. acuta* and *G. parvus*, the most ubiquitous species, were the less influenced by the range of environmental conditions measured. Such modelling issues on the abundance of very rare or very common aquatic macroinvertebrate taxa have already been underlined (Dedecker et al. 2004). Increasing the number of observations for the less frequent species could enhance the quality of the habitat models. A more complete habitat spectrum could be sampled and other explanatory variables could be tested to enhance model quality. For instance, Mérigoux et al. (2009) showed that *D. polymorpha* and *D. tigrina*, have pronounced hydraulic preferences in the main channel of the Rhône River.

Limitations in the habitat modelling for alien species could also originate in the presence of cryptic species. *P. acuta* was the most ubiquitous species among the eight alien species. Two *Physella* species (*P. acuta* and *P. heterostropha*) were considered to be present in that part of Europe (Glöer et al. 1992). However, Dillon et al. (2002) showed that populations of *P. acuta* and *P. heterostropha* were not reproductively isolated. An interpretation of the poor quality of the results could be that, although not reproductively isolated, *P. acuta* and *P. heterostropha* represent two "forms" with potentially contrasted preferences. Once mixed, because of the difficulty of morphological separation, the "taxa" *P. acuta* considered here might appear to have no differentiation along the lateral connectivity gradient.

A similar concern could be applied to *C. fluminea*. Renard et al. (2000) demonstrated by molecular differentiation, the existence of a third distinct species in the French Rhône River, different from *C. fluminea* and *C. fluminalis*. The existence of such cryptic species does not seem uncommon. Indeed, in the Rhine River, two *Corbicula* morphotypes with few intermediates were also distinguished (Pfenninger et al. 2002). However, results concerning *C. fluminea* were significant and this species obtained the best model quality. The U-shaped response to the light availability gradient could be interpreted as a sign of two co-occurring species or ecotypes, each being favoured at the two extremes of this gradient. Consequently, such confusions of "forms" or species could lead to different types of response (apparent indifferentiation along the gradient as in *P. acuta* or U-shaped response as in *C. fluminea*) depending on the degree of coexistence between the "forms". Spooner and Vaughn (2009) indicated that mussels can occupy different "thermal niches", temperature being a mediator for resource. *Corbicula* forms could have different abilities in assimilating available food, according to temperature (Mouthon 2003). As water temperature is largely correlated to light availability, it could be another explanation for the U-shaped response of *C. fluminea* to the light availability gradient. Moreover, even within populations, Williams and McMahon (1986) showed that life-history tactics could vary greatly between years, according to variations of water temperatures and primary productivity. Further investigations and particularly molecular analyses need to be performed to clarify such issues. For other alien species, such investigations allowed to clarify taxonomic uncertainties. For instance, analyses implemented on *Dikerogammarus* invaders in central European rivers separated *D. villosus* from *D. haemobaphes* and confirmed the hypothesis that *D. villosus* replaced the previous invader *D. haemobaphes* (Müller et al. 2002).

The main river channel as dispersal route for alien species

The French Upper-Rhône floodplain is situated between two potential sources of colonisation for the aquatic alien species (see Fig. 1). An important upstream source is Lake Geneva. Large lakes undergo important shipping activities that contribute to alien species dispersal (Johnson and Padilla 1996). Further, the Rhône River downstream in the city of Lyon is connected to the Rhine River through the Saône River. This dissemination pathway is another source of colonisation for aquatic macroinvertebrates in the Upper-Rhône floodplain (Fruget 2003). All alien species found in the study are holobiotic and their mode of dispersal is, for most of them, passive

(Kinzelbach 1995). Even though we could expect that the principal source of colonisation enabling them to reach the Upper-Rhône floodplain is Lake Geneva, observations for some species contradict this hypothesis. Indeed, *C. fluminea* was first observed in the Upper-Rhône floodplain in the nineties whereas it has only been collected as recently as 2007/2008 in Lake Geneva (Lods-Crozet, personal communication). Similarly, *D. polymorpha* was observed after 1852 in the floodplain and only since 1962 in Lake Geneva (Binder 1965). *D. polymorpha* was probably introduced in Lake Geneva on the hull of boats (Binder 1965). Consequently, both colonisation pathways (from Lake Geneva and from the Rhine River via the Saône River) play an important role in the species introduction and spread in the Upper-Rhône floodplain. However, the main river channel, through direct lateral connections with the floodplain, or during flood events, is the principal dispersal route for alien species into the floodplain. This assumption is in accordance with the results for almost all the species. Nevertheless, for the most abundant species in the most disconnected channels (*G. parvus*) other dispersal strategies must be involved. *G. parvus* inhabits pools, ponds or lakes (Meier-Brook 2002) and is abundant in floodplain channels rich in vegetation and never reached by floods. Studies have demonstrated that alien aquatic macroinvertebrates could also be dispersed either internally or externally by waterbirds (Green and Figuerola 2005) and terrestrial mammals (Vanschoenwinkel et al. 2008). These types of dispersal mechanisms could probably play an important role in the dispersal of the small plant-associated *G. parvus* at the floodplain margins.

Restoration impacts on alien species

Since the data were collected, several floodplain channels have been restored, either by reconnection to the main channel or by dredging and deepening. Tree harvesting and replanting also occurred. Except for *P. acuta*, the degree of lateral connectivity was the most influential variable for the occurrence of the alien species found. Restoration by reconnection to the main channel will increase the mineral substrate diversity and reduce both the BOM quantities and aquatic vegetation cover. We can therefore expect that such modifications will favour species like *P. antipodarum*, *C. fluminea* and, on the contrary limit *G. parvus*. Alien species are thus not expected to respond uniformly to restoration works. However, Paillex et al. (2009) showed, in the same study sector, that increasing the lateral connectivity by restoration favoured alien species richness and relative abundance. This type of restoration work consequently facilitated alien macroinvertebrate species dispersal. These findings also confirm the fact that the main channel is a potential dispersal pathway for most of the alien species in the lateral dimension of the floodplain. Light availability was less influential upon species distribution than the lateral connectivity gradient. However, restoration work, which results in local tree felling, can increase solar access to the channels. In other places, tree plantation is also used as part of the restoration process and will modify solar access, but at a slower rate. Our models indicate that forest harvesting could favour the abundance of alien species, with the exception of *C. fluminea*.

Consequences of floodplain restoration cannot be considered in isolation from the potential impacts of climate changes. Indeed, the light availability gradient which contributes to the heat balance of the channels and the lateral connectivity gradient will be influenced by climate changes. Current climate changes will cause warmer water temperatures and less predictable alterations of the streamflow regime (floods and droughts) (Rahel and Olden 2008). Analyses of the influence of the 2003 heatwave on the French Saône River, and of its impacts upon mollusc communities, showed *D. polymorpha* and *C. fluminea* to be more resilient to heatwaves than other species of molluscs (Mouthon and Daufresne 2006). *P. acuta* can also be regarded as tolerant to high water temperatures since it was introduced in warm regions of Africa, the Mideast and South Asia (Falkner et al. 2002). Moreover, studies undertaken between 1985 and 2004 on the entire French Rhône River demonstrated that floods and the 2003 heatwave favoured the development of eurytolerant and alien taxa of aquatic macroinvertebrates (Daufresne et al. 2007).

Consequently, we recommend assessing the existence of alien species potentially favoured by an increase of light availability before implementing forest harvesting works. Moreover, we recommend maintaining a high diversification of hydrological conditions and consequently high habitat diversity in order to minimise the rate of successful adaptation of

alien species. However, the conjunction of climate change and restoration works might act synergistically to favour the spread of alien species. As a consequence, we can expect in the future an increase of the number and the abundance of alien species in the French Upper-Rhône floodplain and in other mid-European rivers.

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